The Systematics of the Prickly Sculpin, *Cottus asper* Richardson, a Polytypic Species

Part II. Studies on the Life History, with Especial Reference to Migration[1]

RICHARD J. KREJSA[2]

ABSTRACT: The occurrence of a downstream spring migration of weakly-prickled *Cottus asper* in coastal streams is confirmed and documented. Successful intertidal spawning and incubation is followed by a pelagic larval stage of about one month. Metamorphosis occurs and the prejuveniles settle to the bottom to feed in the estuarine portion of the river. An upstream migration of adults precedes that of the young-of-the-year in late summer. During the non-migratory phase, prickly sculpins are located in the low gradient, low velocity portions of coastal streams.

Densely-prickled *Cottus asper* living in distant inland waters, where access to the sea is almost impossible, undertake only local migratory movements. Densely-prickled forms living in some inland lakes and streams relatively close to the sea, where access to the sea is open and relatively easy, do not migrate seaward but undertake only local movements to spawn in fresh water. The present study discusses differences in migratory behavior between "coastal" and "inland" prickly sculpins.

THE EXISTENCE of a seaward spawning migration of prickly sculpins in coastal streams has been suggested, or implied, for at least 30 years (Taft, 1934; Pritchard, 1936; Sumner, 1953; Shapovalov and Taft, 1954; Hunter, 1959; and McAllister and Lindsey, 1959). Although some of these authors have observed the presence of reproductively mature *Cottus asper* in the intertidal areas of coastal streams, none has demonstrated that intertidal spawning actually occurs.

Populations of *C. asper* occurring in lakes and streams far enough inland to preclude the possibility of an annual seaward spawning migration are presumed to spawn in fresh water. The approximate or exact spawning sites of some of these populations have now been determined from the presence of larvae (Nicola Lake, British Columbia), and egg clusters or gravid females (Pothole Lake, near Merritt, British Columbia). Other localities are close enough to the sea to imply the existence of a short seaward migration on the part of the *C. asper* populations living therein, but access to the sea is prevented by natural or man-made barriers, e.g., at Buttle Lake and Horne Lake, on Vancouver Island, British Columbia. Spawning of prickly sculpins in these areas is necessarily restricted to fresh water.

Still other localities, frequented by migratory salmonids, are close enough to the sea to permit a seaward migration on the part of *C. asper* living there, but it does not occur. For example, these spawning sites of the following prickly sculpin populations in the lower Fraser Valley in British Columbia are known from capture of gravid fish and/or egg masses: South Alouette River; Kenworthy Creek and Chilqua Slough (both are inlet streams to Hatzic Lake); Squakum Lake (Lake Erroch); and Cultus Lake. In addition, spawning fish have been captured in inlet streams of Skidegate Lake, in the Queen Charlotte Islands, along with migratory juvenile salmonids. The outlet of Skidegate Lake is only about 13 miles from the sea. A newly hatched larva of *C. asper* (?) has been taken in a

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[2] Institute of Fisheries, University of British Columbia, Vancouver, Canada. Present address: Department of Anatomy, College of Physicians and Surgeons, Columbia University, New York, N.Y.

plankton net in the Second Narrows region of Owikeno Lake (about 30 miles from the sea), on the coast of central British Columbia. It is presumed that the parents spawned in fresh water.

MATERIALS AND METHODS

To document the supposed occurrence and to determine the success of intertidal spawning of prickly sculpins in the coastal streams, the Little Campbell River (Fig. 1, site 2) was chosen as a study stream. In 1960–1961, a series of 18 permanent collecting sites (Fig. 2) was sampled at biweekly intervals for a period of one year, and at monthly intervals for an additional six months. The lower reaches of the river, stations C-1 to C-3, were also sampled several times in late winter and early spring of 1962 and 1963, to obtain live specimens for laboratory studies. Additional live specimens for use in laboratory studies were collected from the following localities (Fig. 1): site 1, Nile Creek and Big Qualicum River, Vancouver Island; site 3, South Alouette River; site 4, Kenworthy and Edwards creeks (Hatzic Lake); site 5, Sweltzer Creek (outlet of Cultus Lake); and site 6, Squakum Lake (Lake Erroch).

A 3 mm-mesh, woven-nylon seine, 3 m wide $\times$ 2 m deep, was mounted on collapsible telescoping aluminum poles and used for all field collections. Salinities were measured with density hydrometers.

SAMPLING LOCALITIES AND STUDY STREAM

The primary study area was the Little Campbell River (Campbell Creek), which is approximately 15 miles long and empties into Semiahmoo Bay between White Rock, British Columbia and Blaine, Washington (site 2, and inset of Fig. 1). The stream's drainage area is approximately 28 square miles.

Collection sites are shown in Figure 2. Station 0-1 is located on a sand-mud flat outside the main river channel. Station C-0 is located below the railroad trestle at the mouth of the river in the main channel, station C-1 about 50

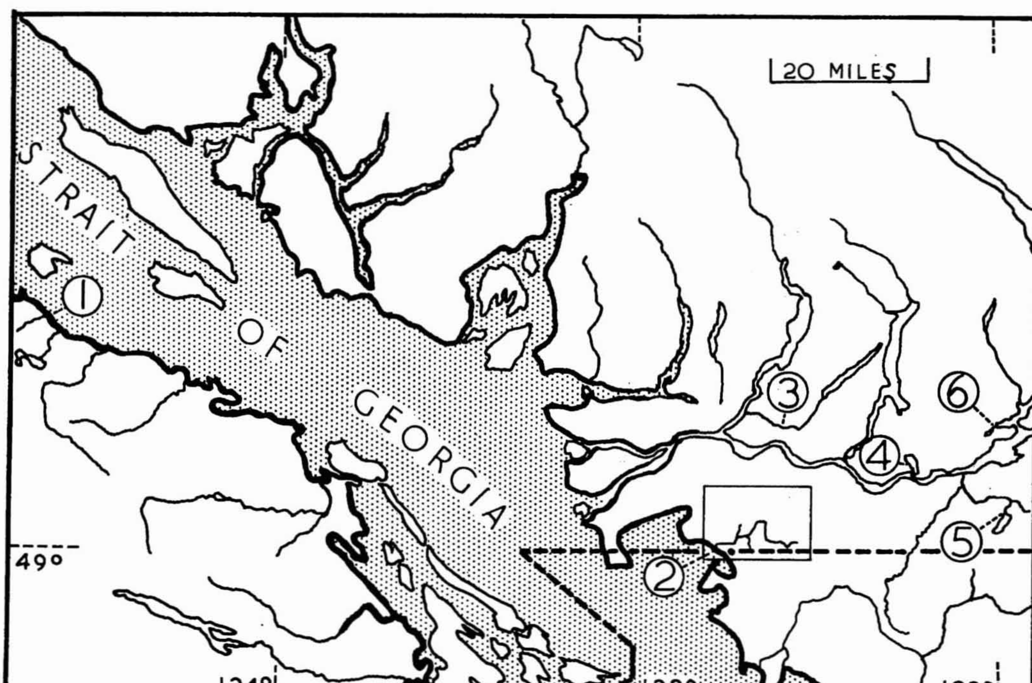

FIG. 1. Localities for spawning populations of *Cottus asper* used in life history studies. Site 2 (inset) is expanded in Figure 2. Other site localities are listed in text.

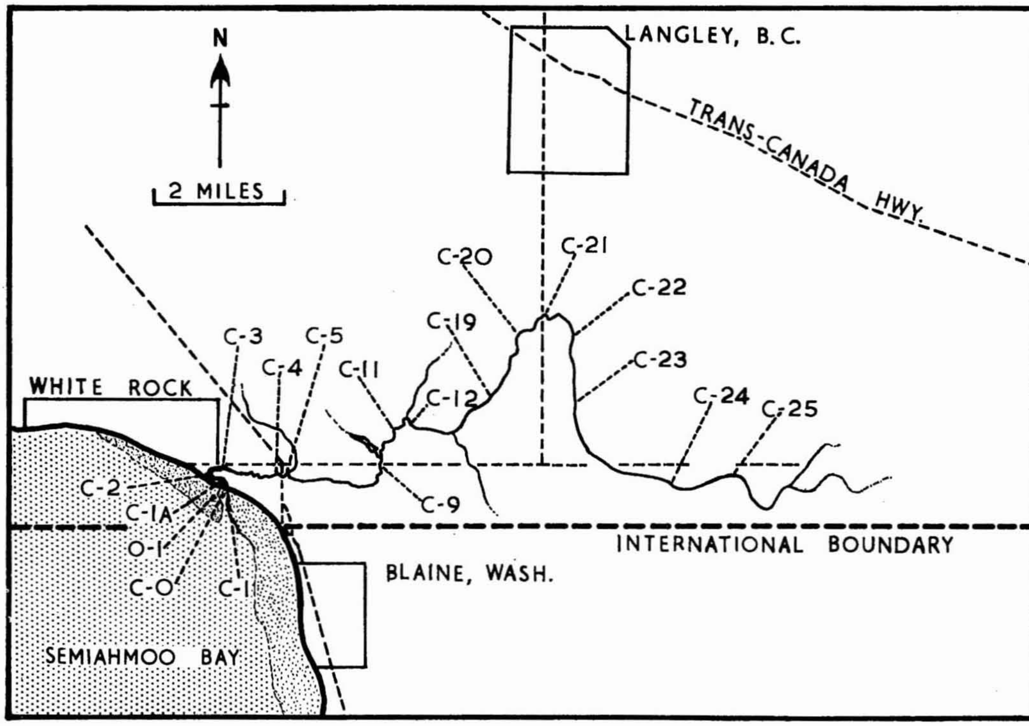

FIG. 2. Collection sites within the Little Campbell River.

yards inside the mouth, and station C-1A about 75 yards inside the mouth. Station C-2 is located $\frac{1}{4}$ mile, and C-3 $\frac{1}{3}$ mile, from the mouth. Figure 3 shows the collection sites in relation to stream gradients, and maximum upstream effects of tidal fluctuations in salinity and depth. Stations C-0 through C-9 are all subject to tidal fluctuations in depth, whereas stations C-0 through C-3 are tidally inundated with mixohaline waters.

Barnacles (*Balanus* sp.) are found at stations C-0 through C-3, and permanent beds of the oyster *Crassostrea gigas* are located between stations C-1 and C-1A, and at C-2. Typical fish associates in areas C-0 through C-3 are *Leptocottus armatus, Platichthys stellatus,* and, throughout the summer, young-of-the-year *Cottus aleuticus. Oligocottus maculosus* and *Clinocottus acuticeps* are commonly found upstream as far as station C-2.

RESULTS OF FIELD STUDIES

The prickly sculpin is distributed primarily in the lower 4 miles of the Little Campbell River. Especially in spring, 1961, an increased number of *C. asper* were present in the lower reaches of the river, around the spawning site (station C-2). Over the first 9-month sampling period, no *C. asper* were captured in stations upstream of C-22. With three exceptions, none was taken in the fast-flowing, high gradient area of the stream below C-20 and above C-11 (Fig. 3). This area is densely populated with the coast range sculpin, *Cottus aleuticus.* Figure 4 illustrates the disjunct distribution of yearlings, subadult, and adult prickly sculpins.

From late February to early March the prickly sculpin undertakes a migration downstream to the estuary. The only area in the lower 4 miles of stream in which suitable spawning substrate (large cobbles, flat rocks) occurs is a stretch about 100 yards long lying $\frac{1}{4}$ mile upstream from the mouth (station C-2, Figs. 2 and 3). The males, which come into spawning condition earlier in the season than the females (see below), select nesting sites under large cobbles or flat rocks in areas of the stream bed with current velocities equal to or less than 1 cubic ft/second (at low tide). Apparently it is im-

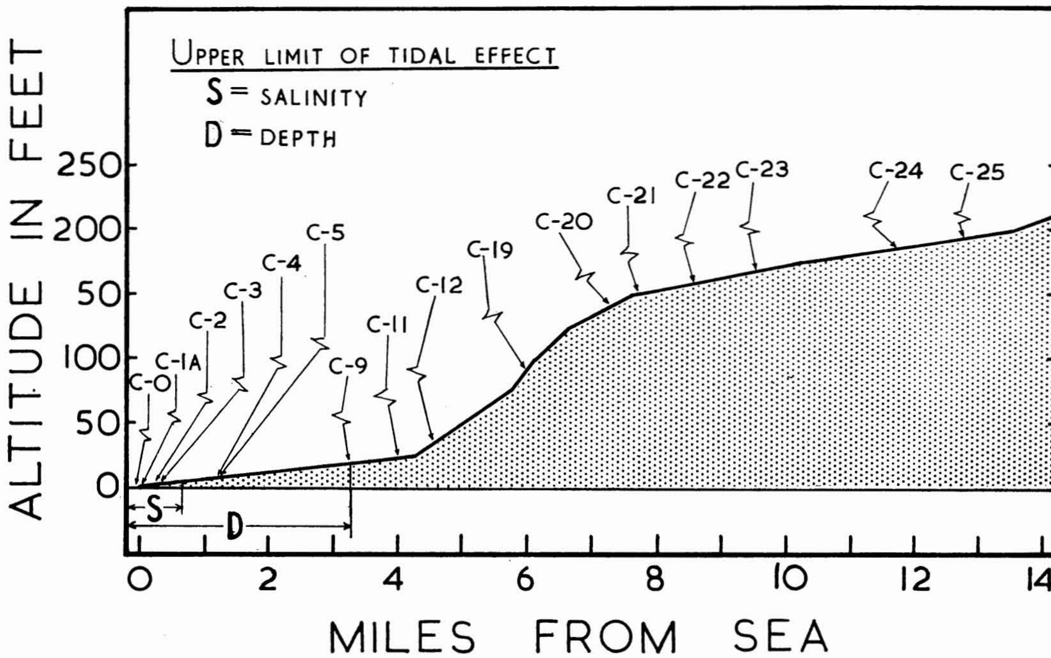

FIG. 3. Little Campbell River collection sites in relation to stream gradients and tidal influence. See text for explanation.

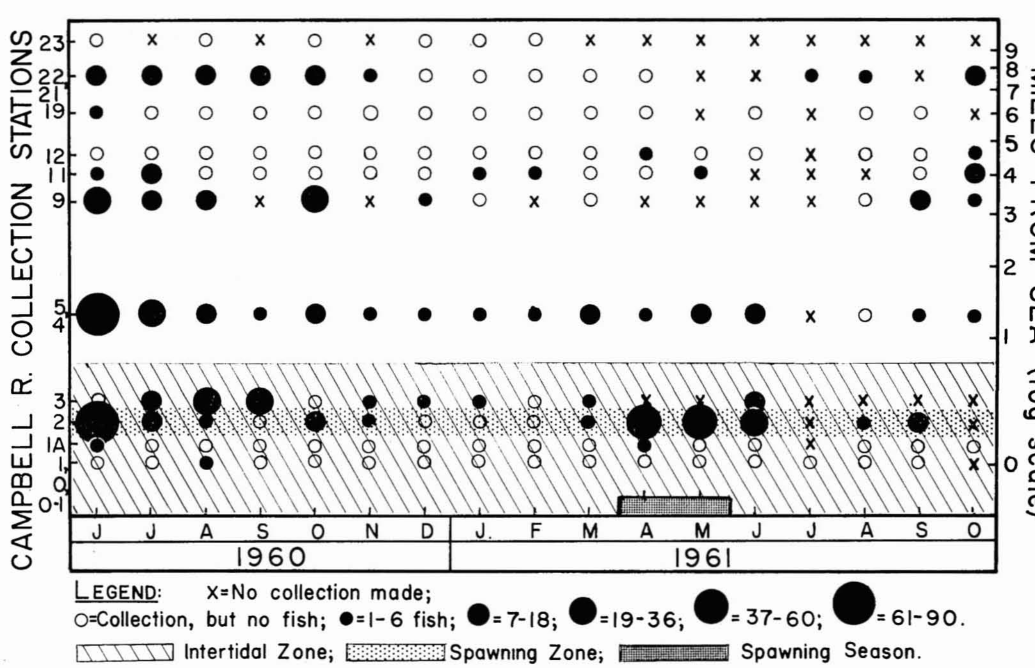

FIG. 4. Monthly distribution of yearling, subadult, and adult *Cottus asper* within the Little Campbell River. Data taken from pooled biweekly samples representing results of 700 seine hauls.

portant that the substrate surface be relatively rough in texture, since the adhesive eggs adhere only temporarily to a smooth surface such as glass or plastic. Old automobile exhaust pipes, or muffler tubes, are "preferred" nesting sites when available in the environment (as they are in the Little Campbell River).

Females aggregate upstream (about station C-3) above the main spawning area and then move individually onto the spawning beds where they display to, and are courted by, males both outside and inside their nests. After a male selects a female to occupy his nest, further courtship and prespawning behavior occurs within the nest. The adhesive eggs are laid in a jelly-enclosed cluster on the ceiling of the spawning chamber. Ovariotomy of preserved gravid females from throughout the distributional range of *C. asper* yielded counts of 336 mature oöcytes in a 49.5-mm S.L. female, to 5,652 mature oöcytes in a female of 119.5 mm S.L. The largest female examined was 192 mm S.L., but she was spent. A conservative estimate of the number of mature oöcytes would be about 10,000 for this female. Numbers of viable eggs, in masses collected in the field, varied from 700 to 4,000 per cluster. However, one male may court and successfully mate with as many as 10 different females (personal observation). As many as 10 egg masses, in varying stages of development from newly-fertilized to near-hatching, have been found in the nest of a single brooding male. An estimated 25,000–30,000 eggs were present in this one nest.

After spawning, the spent females leave, or are chased from, the nests and they again aggregate above the spawning areas and begin feeding. The males remain in the nests, fanning and protecting the eggs, and do not eat until hatching of all egg clusters is completed. Much of the courtship and prespawning behavior, as well as most of the paternal brooding behavior through hatching, has been documented and will be reported elsewhere.

Laboratory studies on the behavior of *C. asper* larvae, done in extension of salinity-tolerance experiments (also to be reported elsewhere), indicate that at 12° C the larvae 5–7 mm in total length begin swimming immediately upon hatching. They remain pelagic, as lightly-pigmented transparent larvae, for a period of 30–35 days before metamorphosing and settling to the bottom.

Figure 5 illustrates numbers and distribution of *C. asper* young-of-the-year, 12–25 mm S.L., taken in a total of 700 seine hauls. In late spring and throughout the summer, the newly metamorphosed young-of-the-year are found in great numbers around and below the spawning site. The concentration is greatest around station C-1A, where there is a bed of fine, pea-size gravel adjacent to a large oyster bed. In mid-summer, there is a definite upstream migration of the young-of-the-year. In both 1960 and 1961, the increasing abundance of young-of-the-year at stations C-4 and C-5 was correlated with the decreasing abundance of specimens in the estuarine areas of the river (Fig. 5).

Spawning Period and Temperature Relationships

Egg clusters were collected from several localities in the lower Fraser Valley (cf. Fig. 1) and in the Little Campbell River. Gonads were examined in over 1,100 preserved museum specimens from all latitudes within the distributional range of *C. asper*. These data indicate that egg deposition begins in the south of the distribution range (low latitudes) in February, and progresses northward until late July. Males usually attain full reproductive maturity about a month before, and remain in spawning condition for almost a month after, the period of oviposition in females. Gravid females have been found over a 4-week period in Squakum Lake, and a 6-week period in the Little Campbell River. Ripe males have been taken over an 8–12 week period, respectively, in these same localities.

The earliest date on which a ripe male, in nuptial dress and with flowing sperm, was collected is February 6, in San Francisco Bay. The earliest collection of gravid females was in Waddell Creek, California, on February 24. In the north end of the range, gravid females were taken as late as June 20 in Petersen Creek, near Juneau, Alaska, and on July 22 in streams entering Juskatla Inlet, Queen Charlotte Islands. Gravid females have also been collected from Middle River, near Takla Lake, on June 28, and from Meziadin Lake, B. C., on July 25.

Field records and personal observations indi-

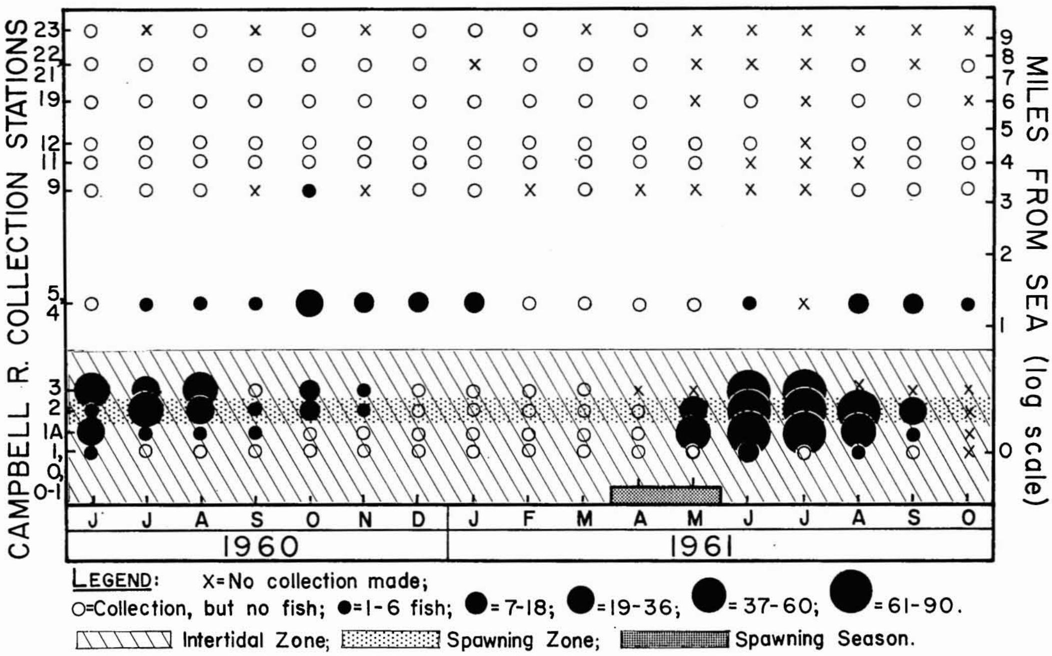

FIG. 5. Monthly distribution of young-of-the-year *Cottus asper* within the Little Campbell River. Data taken from pooled biweekly samples representing results of 700 seine hauls.

cate that natural spawning temperatures range from 8° to 13° C. Egg-rearing experiments at various temperatures resulted in complete mortality at 18° C, less than 50% survival at 15° C, and greater than 85% survival at 12° C. Control of lower temperatures was beyond the limitations of available equipment.

The annual mean range of ambient temperatures experienced by inland populations of *C. asper* is twice as great as that experienced by coastal populations at the same latitude (Krejsa, 1965:109). The monthly mean temperature range between northern and southern localities is from 8.8° to 19.5° C on the coast, and from 9.6° to 29.6° C inland. *A priori*, one might expect that inland populations would experience a greater range of developmental temperatures than do coastal populations. Apparently, however, they do not. When monthly mean temperatures, representing inland and coastal localities encompassing the distributional range of *C. asper*, are plotted against latitude, the mean temperature differences between inland and coastal localities during the spawning period are almost negligible (Fig. 6). In fact, the empirically determined, average spawning temperature range of 8° to 13° C (shaded bar, Fig. 6) can be followed as a thermal "wave" progressing through inland and coastal localities from the south in February, to the north in June. Approximate spawning times, determined from examinations of gonadal condition in more than 1,100 specimens from all latitudes, are in general agreement with this south-north progression although the latitudinal range over which spawning occurs in March, April, and May is remarkably consistent (Fig. 6).

Theoretically, inland forms have a shorter period of exposure to spawning temperatures of 8° to 13° C than do coastal forms (Fig. 6). This supposition has been borne out by field data from the two most frequently collected spawning sites, Squakum Lake and Little Campbell River.

According to Figure 6, the inception of spawning in inland streams should lag behind that of coastal streams at similar latitudes. This is because upstream or inland areas remain colder for a longer period than do coastal areas. This is apparently true in the lower Fraser Valley. For example, the following localities are all within 15′ of 49° N, and gravid females and/

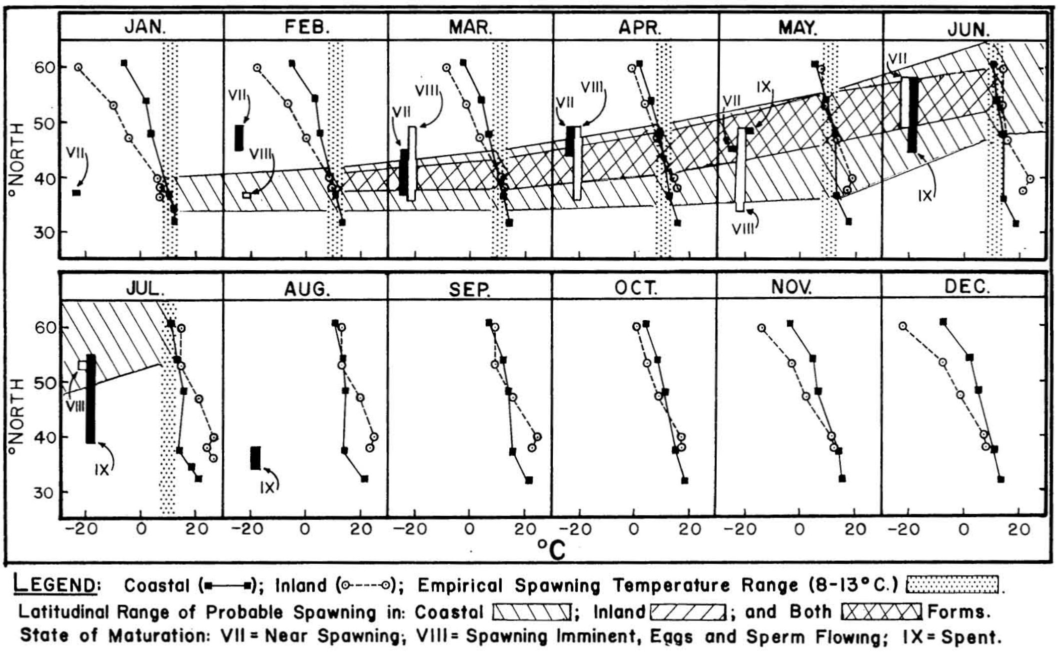

FIG. 6. Monthly mean temperatures in °C arranged by latitude for coastal and inland localities encompassing the distributional range of *Cottus asper*. Solid or unfilled vertical bars, left side of each panel, indicate actual ranges of latitude over which specimens have been found in a given state of maturity. Temperature values after Krejsa, (1965:109).

or eggs have been collected from them during the following dates: March 7 to May 10 in Little Campbell River (122° 46′ W); March 25 to April 15 in South Alouette River (122° 35′ W); and April 30 to May 27 in Squakum Lake (122° 00′ W).

DISCUSSION

The present study confirms the existence of a downstream spawning migration of the prickly sculpin in the Little Campbell River. It not only documents the occurrence of intertidal spawning in this coastal population of *C. asper,* but indicates that this spawning is successful. By extrapolation, the success of intertidal spawning in other coastal streams of the Pacific coast, where catadromous populations of *C. asper* have been reported, is indicated.

The lack of a seaward migration in "inland" populations with or without immediate access to the sea is also documented. In these populations, fresh-water spawning is the invariable norm.

Krejsa (1965) has discussed the evidence for recognizing a genetic distinction between "coastal" and "inland" populations of prickly sculpins based on morphology (prickling patterns) and geographic distribution. Bohn and Hoar (1965) have presented physiological evidence based on a comparison of iodine metabolism in "coastal" (Little Campbell River) and "inland" (Lagace Creek, Hatzic Lake) forms of *C. asper*. They concluded that the two populations studied have diverged genetically in their physiological capacities to deal with water of different electrolyte content.

If the above evidence is considered in light of the present study, the following picture emerges. Weakly-prickled *C. asper* living in coastal streams having open access to the sea undertake a downstream migration to the estuarine regions where eggs are spawned, hatched, and the young are reared successfully. Densely-prickled *C. asper* living in distant inland streams, where access to the sea is almost impossible, undertake only local migratory movements. But densely-prickled forms living in some inland lakes and streams relatively close to the sea, where access to the sea is open and relatively easy to achieve, do not migrate seaward. They also undertake only local movements and spawn within the fresh-water system in which they are found. Such primary differences in behavior, correlated with distinct differences in prickling patterns, geographical distribution, and iodine metabolism, further corroborate the contention that "coastal" and "inland" forms of *C. asper* are genetically distinct.

Figure 5 shows a lag of about two months in the appearance of young-of-the-year *C. asper*, 12–25 mm S.L., after the first recorded spawning in March. Water temperatures in March are normally from 8° to 10° C. Eggs spawned early in March probably have an incubation period several days longer than the 15–16 day period found to be typical at 12° C in the laboratory. The lag shown in Figure 5 probably is due to an incubation period of 3 weeks followed by a pelagic larval stage of 4–5 weeks. Plankton tows taken during late April in the shallow back-eddies of the stream have captured a few larvae 9–10 mm S.L. (not recorded in Fig. 5).

An upstream migration of adults precedes that of the young-of-the-year in late summer. This is probably related to the food habits of the two groups and also to the fact that a later return of the young-of-the-year coincides with lower water levels in the stream, when reduced water velocity facilitates access upstream.

The usual spawning temperature range for *C. asper* is from 8° to 13° C. It is assumed that in most populations spawning is initiated within this 5° range of temperature, which proceeds in somewhat of a thermal "wave" from south to north in both inland and coastal localities (Fig. 6). This is not to say that they all spawn at the same temperature within the range. Furthermore, because the monthly rate of increase of ambient temperature is greater in the north, the duration of exposure of prickly sculpin eggs to any given temperature within the 5° C temperature range may be shorter. Eggs subjected to these conditions presumably would have a faster development than eggs which developed under relatively more thermostable conditions, such as occur in the south of the distributional range. Low meristic counts are generally (although not invariably) associated with faster rates of development. An experimental analysis of temperature-determined morphological differences is needed, especially of meristic differences, between "coastal" and "inland" populations of *C. asper* at the same latitude and between fishes from the north and south ends of their respective ranges. The implications and the desirability of such studies in determining the validity of the proposed genetic distinction between "inland" and "coastal" populations are obvious. The existing meristic evidence (Krejsa, 1965) is equivocal.

SUMMARY

1. The stream studied, the Little Campbell River, is a small coastal stream, the lower $\frac{1}{2}$ mile of which is subject to tidal inundation of mixohaline waters.

2. In late winter and early spring, the adults and juvenile prickly sculpins migrate downstream to the estuarine region of the Little Campbell River, the only region in the lower 4 miles in which suitable spawning substrate is available.

3. Males set up nesting sites under large cobbles and rocks, and courtship occurs both outside and within the nest.

4. Spawning occurs from March throughout early May.

5. Newly-hatched larvae begin swimming immediately and remain pelagic for a period of 30–35 days before metamorphosing and settling to the bottom.

6. In May, metamorphosed young-of-the-year (approximately 12 mm S.L.) begin appearing only in those collections taken in the estuarine portion of the river. They occur in great abundance until September, when the numbers decrease in the estaury and increase in upstream, nonestuarine waters.

7. During the nonmigratory phase of its life history, the prickly sculpin population in the Little Campbell River is distributed primarily in the low gradient, low velocity, portions of the stream.

8. Within any given population of prickly sculpins, the males are reproductively active longer, in a given season, than the females. The period of reproductive activity of both sexes is

more extensive in "coastal" populations than in "inland" populations.

9. The empirically determined, average natural spawning temperature of *C. asper* is from 8° to 13° C for both "coastal" and "inland" populations. Within this range of temperature, egg deposition begins in February in the south of the distributional range and progresses northward until July.

10. The existence of catadromous "coastal" populations and nonmigratory "inland" populations is indicative of genetic distinction between them. This contention is further strengthened by the existence of parallel differences in morphology, physiology, and geographic distribution.

ACKNOWLEDGMENTS

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ADDENDUM

Since this manuscript was submitted for publication, Mr. Gerald D. Taylor has presented an excellent statistical analysis of experimental field and laboratory studies on the interrelationships of *Cottus asper* and *C. aleuticus* in the Little Campbell River.[1] His thesis forms a valuable contribution to our present knowledge of sculpin ecology. Most of his conclusions expand and elaborate upon many of the observations reported above. However, his study opens up the possibility that some of the prickly sculpins in the Little Campbell River do not spawn in the lower estuarine portion of the stream but upstream "in close proximity to spawning *C. aleuticus*."

In other nearby coastal streams where stream profiles are different, I have collected reproductively active *C. asper* and *C. aleuticus* in close proximity, but never have I done so in the Little Campbell River. I am skeptical of Taylor's statement primarily because his collections were carried out only during 5 months (of a 7-month period: August to November, 1965, and February, 1966), all of which are outside the normal spawning season of most *C. asper* as documented above. Taylor's study will be given more consideration in a future report on the behavior of *C. asper* and *C. aleuticus*.

[1] Taylor, G. D. 1966. Distribution and Habitat Responses of the Coastrange Sculpin (*Cottus aleuticus*) and Prickly Sculpin (*Cottus asper*) in the Little Campbell River, British Columbia. Unpublished M.S. thesis, Department of Zoology, University of British Columbia (December, 1966).